Ball Mountain Revisited: Anomalous Species Richness of a Montane Barrier Zone

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Abstract. Ball Mountain, located in eastern Siskiyou County, northern California, has one of the richest documented butterfly faunas of any area its size in temperate North America, now numbering 101 entities (species and subspecies) recorded in 18 collecting trips over 8 years. It has a clear faunistic relationship with the Warner Mountains, some 225 km distant. Ball Mountain separates two different climates, and its faunal richness is enhanced by the presence of vicariant species or subspecies pairs in several complexes on its eastern and western slopes. The possible role of "mass effect" in generating butterfly species richness is discussed.

What determines species richness, the number of species of a given taxonomic group in an area? A vast literature has grown up in ecology attempting to answer this question, as any introductory textbook in that discipline attests; the subject has gained in urgency when applied to conservation problems. Particular efforts have been devoted to comparisons of species richness along various gradients, such as between tropical and temperate regions. Anomalously low or high species counts within a region may be useful in identifying important factors associated with those sites which affect species richness.

Ball Mountain is a 2330 m basaltic volcano of Pliocene age located in eastern Siskiyou County, northern California, 47 km N of Mount Shasta. Its geographic and vegetational characteristics are described in Shapiro (1986), along with a summary of its principal butterfly habitats. A butterfly faunal survey of Ball Mountain was initiated in 1983, triggered by its intriguing location as an isolated high point in a biogeographically complex region. An initial visit demonstrated extreme telescoping of the altitudinal vegetation belts, important slope- and exposure-mediated vegetational discontinuities, and the presence of numerous rare or disjunctly-distributed plant species. (Although Goosenest is a larger volcano at 2524 m, it is geologically younger and much less well-vegetated.) As of late 1985 the accessible areas above 1500 m, encompassing representatives of all identified butterfly habitats, had been collected seven times: Shapiro (1986) reported 68 species, a rich fauna for an area less than 150 km^2 even given the pronounced vegetational zonation.

Since then Ball Mountain has been collected 11 more times, raising the total taxa recorded there to 101. Many of the additional taxa were found to be intensely localized in sites on the eastern and southern sides of the mountain. Although rigorous comparisons are not available, it is evident that this must stand as one of the richest butterfly faunas, for its area, in temperate North America. Shapiro, Palm and Wcislo (1981) recorded 115 species in the Trinity Alps, encompassing much more topographic and vegetational diversity in an area of 2030 km^2. No 150-km^2 segment of the Trinities is likely to contain 100 species. The richest butterfly fauna recorded in California (and perhaps temperate North America) is that of Donner Pass in Placer and Nevada Counties (Sierra Nevada, 2100 m), with roughly 115 species in some 50 km^2 (Shapiro, unpublished data, 1972-1990). However, Donner is embedded in a large and topographically diverse mountain range, while Ball Mountain is one of only three mountain "islands" above 2270 m between Mount Shasta and central Oregon, and most of the surrounding country is below 1300 m. Thus the resident portion of its fauna, if montane-endemic, must represent either historic (relict) or recent colonization from substantial distances away. Shapiro (1986) pointed out a distinct endemic element in the Ball Mountain fauna, as well as an apparent connection to the fauna of the Warner Mountains in Modoc County, 225 km to the E.

Subsequent collecting has revealed an even more pronounced Warner Mountain connection in the fauna. The complete collection data for 18 days afield are given in Table 1. Comments follow on some especially interesting additions to the fauna. They should be read in conjunction with Shapiro (1986) and the most relevant major faunistic treatment, Dornfeld (1980) for Oregon. A revised faunal breakdown by families appears in Table 2.

Pieris napi L. — The "parent colony" of the single previous record has been located in the Shovel Creek (E slope) drainage. Only a spring brood has been found, but the phenotype is indistinguishable from the hitherto unique Warner Mountain one. The host plant has not been identified.

Anthocharis sara Lucas. — Previous records were based only on males and were characterized as the nominate subspecies *sara*. Now that females are in hand it appears that they should be assigned to ssp. *thoosa* Scudder or *flora* Wright, with yellowish upperside in the female. Whatever the applicable name, they resemble Warner Mountains ones.

Anthocharis lanceolata Bdv. — Uncommon, but present on both the W and E slopes at 1650-1800 m, primarily in canyons.

Coenonympha tullia Mueller complex. — West-slope specimens fall comfortably into the taxon *eryngii* Henry Edwards. East-slope ones are highly variable, with some approaching *elko* W. H. Edwards. Populations along Prather Ranch Road at the E base of the mountain are especially dense. This may be an intergrade zone. Porter and Geiger (1988) treat several nearby populations as such. Montague (Shasta Valley, west of Ball Mountain) is treated as *eryngii*, while MacArthur and Adin, to the SE, and Goose Lake, just W of the Warners (and nearly due E) are treated as intergrade zones. Specimens from the far W of Butte Valley (Sams Neck-Meiss Lake Road) are mostly very similar to Goose Lake ones.

Oeneis nevadensis Feld. & Feld. — Expected, but first collected only in 1988 as it flies only in even-numbered years; widespread and fairly common.

Cercyonis pegala Fabr. complex. — Occasional specimens of ssp. *boopis* Behr occur on the W slope up to 1850 m. On the E slope the situation is more complicated. The species is very abundant in the lower E-slope canyons and especially at the foot of the mountain, along Sams Neck-Meiss Lake Road, whence it extends into marshy grasslands in Butte Valley. These populations are extremely variable and seem to represent intergrades from *boopis* to nearly typical *ariane* Bdv., with all phenotypes represented in a series of 26 collected 22.VII.1990. They also occur in a range of habitats from open conifer forest and shrubland to grassy swales with no woody vegetation. *Boopis* is common along streams in Shasta Valley W of Ball Mountain and even occurs in alfalfa fields there.

Euphydryas chalcedona near *wallacensis* Gunder. — Common at mid-elevation on both slopes, and indistinguishable from a long series from Cedar Pass in the Warner Mountains. In 1990, under severe drought conditions, this species flew a full month early on Ball Mountain. In June 1991 it reached outbreak abundance, flying by thousands.

Speyeria zerene Bdv. — Abundant. In the Warner Mountains, E-slope populations are of the pale ssp. *gunderi* Comstock and W-slope populations show a complete and very confusing array of phenotypes intergrading from *gunderi* to *conchyliatus* Comstock. With about 60 Ball Mountain specimens on hand it is evident that about two-thirds of this variation exists on Ball Mt.; the most *gunderi*-like phenotypes are missing, but some females are rather clay-colored above and olivaceous, vaguely greenish-brown below and such specimens are not known elsewhere in the region except in the Warners. One possible explanation of this situation is an historic presence of *gunderi* here, later swamped out in pure form through hybridization with *conchyliatus*. Such a scenario is consistent with a Hypsithermal Warner-Ball Mountain connection, discussed below.

Speyeria mormonia Bdv. — Comparison of our series (including six 1990 captures) with specimens from Bidwell Peak in the Warner Mts. (21.VII.1985, *leg.* C. Hageman) shows Ball Mt. specimens consistently lacking the greenish VHW basal flush usually present in the Warners. In this regard they match northern Sierran material more closely, though on other characters they are essentially intermediate.

Satyrium fuliginosum W. H. Edwards. — Three Ball Mountain specimens: two from Little Shasta Meadow, 21.VI.1987 and 22.VII.1990 and one from the mid-W slope, 24.VII.1987. What is confusing is that the two Little Shasta specimens appear subspecifically different from the other. The W-slope animal resembles Trinity-Eddy ones, while the Little Shasta ones are smaller, intense black on the upper surface, and with the heavily-spotted high-desert facies below. This problem must remain unresolved until breeding can be established, but at least the Little Shasta situation implies residence.

Table 1. Occurrence of butterfly species on Ball Mountain on 18 collecting days, 1983-1991. On all occasions the mountain was sampled comparably except on 4.IX.1987, when increasing cloudiness terminated butterfly activity in early afternoon. *Colias* hybrids are not counted separately in the totals, but named subspecies of polytypic complexes (*Cercyonis pegala*, *Lycaena editha*/*xanthoides*) are. For further information, see text. (Note that 1990 phenology was unusual; low snow pack produced a full month of acceleration at the beginning of the flight season, followed by cold, wet weather in late spring leading to a normalization to a slight deceleration in midsummer.)

	V.10.1990	VI.8.1991	VI.12.1985	VI.21.1987	VI.22.1986	VII.3.1985	VII.12.1988	VII.15.1983	VII.22.1990	VII.24.1987	VIII.10.1983	VIII.10.1985	VIII.23.1986	IX.1.1990	IX.4.1987	IX.4.1988	IX.5.1985	IX.7.1983
Papilio zelicaon	X	X	X		X	X						X						
Papilio rutulus			X		X	X	X		X									
Papilio eurymedon		X			X	X			X									
Parnassius clodius			X	X	X	X			X	X								
Neophasia menapia									X	X		X	X	X	X	X	X	X
Pontia sisymbrii	X																	
Pontia beckerii					X		X	X				X		X	X	X	X	
Pontia occidentalis	X	X	X		X	X	X	X	X		X	X	X	X	X	X	X	X
Pieris napi "Warner"	X	X	X															
Pieris rapae			X				X		X			X	X			X	X	
Colias eurytheme	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X
Colias philodice eriphyle	X	X	X		X	X		X	X		X	X		X		X	X	
(Colias e x p hybrids)		X	X		X	X		X		X	X	X				X	X	
Anthocharis sara sara (?)	X		X															
Anthocharis lanceolata	X				X		X											
Euchloe ausonides	X	X	X	X	X	X			X									
Coenonympha tullia nr. eryngii	X	X		X	X			X	X	X	X		X	X	X	X	X	X
Coenonympha tullia nr. elko									X									
Oeneis nevadensis					X		X		X									
Cercyonis pegala nr. ariane							X		X									
Cercyonis pegala nr. boopis									X				X					
Cercyonis silvestris				X			X		X					X		X		
Danaus plexippus		X			X				X			X		X		X	X	
Limenitis lorquini			X	X	X	X	X	X	X	X	X	X				X		
Adelpha bredowii californica												X		X		X	X	
Vanessa virginiensis	X					X		X				X				X	X	
Vanessa cardui	X	X		X	X			X	X		X	X	X			X		
Vanessa annabella		X			X	X			X		X			X		X	X	X
Vanessa atalanta		X								X								
Precis coenia					X				X			X		X		X	X	
Nymphalis californica			X	X	X					X		X		X			X	
Nymphalis milberti furcillata	X				X				X	X	X						X	
Nymphalis antiopa	X	X	X		X	X			X							X	X	
Polygonia faunus rusticus					X												X	
Polygonia oreas silenus					X													
Polygonia zephyrus	X	X	X		X				X	X	X		X	X		X	X	X
Polygonia satyrus										X								
Phyciodes campestris		X	X	X	X		X		X									
Phyciodes mylitta	X	X	X		X	X		X	X	X		X	X	X		X	X	X
Chlosyne hoffmanni segregata						X												
Chlosyne palla	X	X		X	X													
Euphydryas chalcedona	X	X	X	X	X													
Euphydryas editha ssp.			X															
Boloria epithore			X	X	X	X		X			X							
Speyeria coronis nr. simaetha					X	X	X							X		X	X	
Speyeria zerene nr.conchyliatus				X	X	X		X	X	X	X	X	X	X	X	X	X	X
Speyeria callippe nr.rupestris				X	X	X	X	X	X	X								
Speyeria egleis nr. oweni			X	X	X	X		X	X	X	X	X	X	X		X	X	X
Speyeria atlantis ssp.			X	X	X	X		X	X	X	X	X	X	X	X	X	X	X

	V.10.1990	VI.8.1991	VI.12.1985	VI.21.1987	VI.22.1986	VII.3.1985	VII.12.1988	VII.15.1983	VII.22.1990	VII.24.1987	VIII.10.1983	VIII.10.1985	VIII.23.1986	IX.1.1990	IX.4.1987	IX.4.1988	IX.5.1985	IX.7.1983
Speyeria cybele leto										X								
Speyeria mormonia ssp.														X	X	X	X	
Speyeria hydaspe nr.purpurascens				X	X	X		X	X	X	X	X		X	X		X	
Strymon melinus	X													X				
Satyrium saepium					X				X	X	X			X		X		
Satyrium sylvinus				X	X				X	X								
Satyrium californica				X	X				X									
Satyrium tetra				X														
Satyrium auretorum				X														
Satyrium fuliginosum				X					X	X								
Mitoura nelsoni	X	X	X	X	X		X		X									
Mitoura spinetorum																		X
Incisalia mossii ssp.		X	X															
Incisalia eryphon	X	X	X		X	X												
Incisalia iroides	X				X													
Lycaena arota							X		X					X		X	X	X
Lycaena heteronea gravenotata									X	X	X	X						
Lycaena rubidus duofacies									X							X		
Lycaena xanthoides/editha								X		X								
Lycaena editha							X		X					X		X		
Lycaena gorgon					X		X	X										
Lycaena helloides	X	X	X	X	X		X				X	X		X		X	X	X
Lycaena nivalis "Warner"				X	X	X	X	X	X	X	X	X						X
Plebeius idas nr. anna/ricei						X	X		X	X	X	X						
Plebeius melissa "Warner"		X			X		X							X		X		
Plebeius saepiolus	X	X	X		X	X		X	X	X	X		X					
Plebeius icarioides	X	X	X	X	X	X			X		X							
Plebeius acmon	X	X		X	X	X	X		X	X			X	X		X	X	X
Plebeius lupini	X		X		X			X	X									
Agriades "glandon" ssp.					X	X		X	X									
Everes comyntas	X																	
Everes amyntula	X	X	X	X	X	X	X	X										
Glaucopsyche lygdamus columbia	X	X				X		X										
Glaucopsyche piasus	X	X	X															
Celastrina argiolus echo	X	X	X	X	X													
Apodemia mormo nr. mormo										X				X				
Ochlodes sylvanoides				X			X	X	X	X	X	X	X	X		X	X	X
Polites sonora			X	X		X	X	X	X	X	X			X				
Polites sabuleti														X		X		
Atalopedes campestris													X					
Hesperia "comma complex"							X		X		X			X		X	X	
Hesperia lindseyi				X	X													
Hesperia juba	X	X	X		X										X	X	X	X
Hesperia columbia	X				X													
Amblyscirtes vialis				X														
Thorybes mexicana aemilia					X													
Pyrgus ruralis	X		X		X													
Pyrgus communis	X				X				X	X			X				X	
Epargyreus clarus				X														
Erynnis icelus			X															
Erynnis persius	X	X			X		X											
Erynnis propertius	X	X	X	X	X	X		X			X						X	
TOTALS	38	33	36	35	59	32	27	26	50	30	25	24	17	32	9	34	32	17

Table 2. Composition by family of some regional butterfly faunas, revised slightly from Shapiro, 1986. The two *Cercyonis* and *Coenonympha* subspecies and *Lycaena editha* and *L. editha/xanthoides* intergrades are counted as separate species, but *Colias* hybrids are not counted. Increases in the Ball Mountain fauna since 1986 are concentrated in Lycaenidae (11 species), Hesperiidae (7) and Nymphalidae (5), but the largest proportional increase was in Satyridae (5). Additions to other faunas since 1986, not otherwise documented, are not included.

Family	Trinity Alps	Mount Eddy	Crater Lake	Ball Mountain
Papilionidae	7	5	4	4
Pieridae	14	7	9	11
Satyridae	4	3	4	6
Danaidae	1	1	1	1
Nymphalidae	31	25	25	29
Riodinidae	1	1	0	1
Lycaenidae	32	27	26	33
Hesperiidae	25	11	11	16
Totals	115	80	80	101

Lycaena editha Mead. — Phenotypically normal *editha*, indistinguishable from Warner Mountain ones, occur from Little Shasta Meadow down the E slope to Sams Neck-Meiss Lake Road, but at low density. Apparent intergrades to *L. xanthoides* Bdv. occur on the W slope from Kuck's Cabin down, the E-most and highest-elevation intergrades yet discovered. Such populations are abundant in alfalfa fields in Shasta Valley (as at Montague), feeding on weedy docks. Apparent intergrades thus occur within 4.5 km of apparently pure *editha*. A male taken at Little Shasta Meadow on 22.VII.1990 is as large as an intergrade but phenotypically *editha*.

Lycaena rubidus Behr. — Occurs in sedgy swales in Butte Valley (seemingly in the same ecological role as intergrading *editha-xanthoides* in Shasta Valley), apparently straying upslope in the E-slope canyons on Ball Mt. The possibility of competitive exclusion among these entities, with dominance possibly mediated by climate, deserves further study.

Lycaena heteronea gravenotata Klots. — Although Shapiro (1986) speculated that this entity might have a different host plant than normal *L. h. heteronea* Bdv., two females were observed ovipositing on *Eriogonum umbellatum* Torr. (Polygonaceae), the usual *heteronea* host in northern California, at the quarry on the mid-W slope on 24.VII.1987 and another at Little Shasta Meadow, 22.VII.90. The very heavily spotted phenotypes figured by Shapiro (1986) have been found in every specimen of this entity seen or collected throughout this study. Four local breeding colonies are known on Ball Mt.

Plebeius melissa W. H. Edwards. — The highly variable populations of this complex in the Warners remain taxonomically unresolved at this writing (S. Mattoon, pers. comm.). All our Ball Mt. *melissa* are of "Warner" phenotypes and are from the E slope above 1550 m, except a female taken 1.IX.1990 on *Haplopappus* flowers on the S slope. There is a *P. idas anna* Edwards - *ricei* Cross population at Martin Dairy and Little Shasta Meadow, 6-8 km away. This population is quite distinct and shows no sign of phenotypic intergradation. Its host plant has not been determined, and it persists at unusually low density for the taxon.

Everes comyntas Godt. — This record is based on a single female taken on the lower W slope on 10.V.1990. Apparent *comyntas* have also been taken at Gazelle in Shasta Valley. Wright's taxon *sissona*, from Sisson (now Mt. Shasta City), was classified by Miller and Brown (1981) as a synonym of *comyntas*, but reclassified by Ferris (1989) under *amyntula* Bdv. The type, if extant, should be examined as both species apparently do occur in far-northern California.

Plebeius saepiolus Bdv. — On 10.V.1990 a very dense population of this species was found unexpectedly on the lower W slope of Ball Mountain, in juniper-Oregon oak-bunchgrass steppe, closely associated with and seen ovipositing on *Trifolium macrocephalum* (Pursh.) Poir. This site was completely dry in July. A series of 26 ?, 4 / (all fresh) reveals a remarkable degree of variability in the underside pattern, tending toward obsolescence but with a few extremely heavily-spotted individuals. The average wing size is the largest I have seen in this species. The existence of this low-altitude (1650-1800 m) ecotype, apparently adapted to a vernal-ephemeral host in a novel dry habitat, demonstrates nicely how little we do know about the northern California butterfly fauna!

Hesperia columbia Scudder. — Apparently resident on the W slope (only?), but only the first brood has been collected. (In Scott Valley double-brooded, as further south in the Coast Range.)

Hesperia juba Scudder. — Taken visiting dandelions pushing through mushy snow below the summit on 10.V.1990; the only other butterfly present was *Pontia occidentalis* Reakirt (extreme vernal phenotypes, newly eclosed). As elsewhere in northern California, this species has a perfectly clear early spring-autumn bivoltinism.

Hesperia comma L. complex. — West slope animals, collected at low density mainly from thistles, are extremely variable phenotypically. East-slope animals and those taken on the south slope with *Polites sabuleti* Bdv. are apparently pure *harpalus* W. H. Edwards in phenotype. They are at much higher density. They are indistinguishable from Cedar Pass (Warner Mt.) series.

Hesperia lindseyi Holland. — Locally common on the W slope only, mostly in juniper-Oregon oak but straying up into mixed-conifer vegetation along roadsides, on *Asclepias* and *Apocynum* flowers. The darkest *lindseyi* are phenotypically similar to light E-slope *harpalus*, but easily separated from them by geography and flight season.

Polites sabuleti Bdv. — Totally absent on the W slope, but common to abundant on the E and S slopes mainly at *Haplopappus* flowers in September (as at Jess Valley in the Warners). Apparently strictly single-brooded, and phenotypically identical to both Warner and N slope Mt. Shasta specimens.

Discussion

Shmida and Wilson (1985) defined a factor contributing to species richness (or "diversity," usually imprecisely used), which they called "mass effect": the establishment of species in sites where they cannot be self-maintaining, but are regularly replenished from nearby permanent populations. Their studies of plant communities in desert washes revealed unstable populations of upland populations whose persistence depends on seed rain from above; such populations appear deceptively "persistent." More or less the same mechanism was also invoked by Heck (1979). Stevens (1989) claimed that, due to the allegedly narrower niches of tropical as against temperate organisms, "mass effect" generated by variance in microhabitats would contribute to high species richness in many tropical environments.

"Mass effect" has been known to community ecologists and amateur naturalists alike for many years, even if not formally named. Almost all regional faunas and floras contain significant numbers of "stray" species which breed occasionally or even fairly regularly—enough to be unsurprising as records, but without being truly permanent members of the biota. Donner Pass, astride the mountain chain separating the montane-Mediterranean Sierran W slope from the much more continental Great Basin, is a natural collector of dispersing butterflies, a fact which accounts for a sizeable chunk of its high species count. Can something of the sort be recognized at Ball Mountain? If so, whence come the dispersers?

Roughly a fifth of the Ball Mountain species list is based on single collections (one or more individuals in one location on one date alone). This superficially suggests Ball Mountain as a collector of dispersers, but the data must be interpreted cautiously. Four of these species (*Vanessa atalanta* L., *Speyeria cybele leto* Behr.—females in late summer, *Atalopedes campestris* Bdv., *Epargyreus clarus* Cramer) are well-known for their dispersal ability or tendency to "stray." Three more are almost always rare, and little is known of their population biology: *Polygonia oreas silenus* W. H. Edwards, *Mitoura spinetorum* Hew., and *Incisalia mossii* H. Edwards. The following species are more or less common nearby at low elevations and stray upslope more or less frequently: from the W: *C. pegala boopis*, *Polygonia satyrus* W. H. Edwards, *Satyrium tetra* W. H. Edwards, *S. auretorum* Bdv.; from the E: *C. p.* cf. *ariane*, *L. rubidus*; from both sides, *Coenonympha*, as well as much commoner species such as both *Colias*. *Thorybes mexicana aemilia* Skinner is mysterious; its hosts (*Trifolium* spp. are abundant and suitable habitats (moist meadows) likewise. *Pontia sisymbrii* Bdv. seems out of place and its status is uncertain. It could conceivably breed on the grassy lava flow near the top of the mountain, but no host has been found.

Among the common species which are probably not permanent residents high on the mountain, but depend on regular recolonization from below, are such "weedy" taxa as *Precis coenia* Hbn., *Plebeius acmon* Westwood & Hewitson;, *Pontia beckerii* W. H. Edwards, and perhaps *Adelpha bredowii* Geyer, as well as the well-documented directional seasonal migrants *Danaus plexippus* L. and *Vanessa cardui* L.

Is Ball Mountain a collector of strays? Below the Juniper-Oregon Oak zone on the W slope the vegetation is disturbed weedy (annual) grassland, with abundant nectar sources in summer and fall (especially *Centaurea solstitialis* L., Compositae, established within the past 15 yr) and narrow corridors of riparian vegetation. To the E in Butte Valley is agricultural land (alfalfa, potatoes), interspersed with shrub-steppe and moist, sedgy swales. Montane forest butterflies dispersing through these habitats would not lack for nectar sources, but would presumably keep moving until they encountered a more congenial (forested) habitat. This is less improbable than appears at first glance, if anecdotal evidence is worth anything. For example, the only *P. oreas silenus* recorded in a 5-yr study of the Trinities and Eddies (Shapiro, Palm and Wcislo 1981 — plus 8 further yr of occasional collecting, AMS, unpublished) was taken in an alfalfa field some 2 km from coniferous forest. Shapiro (1982) reported surprisingly frequent visits to a suburban butterfly garden by species whose breeding habitats were several km away. But the species most likely to move among upland "islands" of forest, *e. g.*, various *Speyeria*, especially female *zerene* and *coronis* Behr, are common on Ball Mt. and give no hint of being dependent on "mass effect" for their continued existence; in the case of *S. zerene*, the phenotypic variability argues quite otherwise unless we assume regular exchange of specimens with the Warners, 225 km away.

A significant component of the faunal richness at Ball Mountain consists of species with Warner Mountains affinities, and this is telling. These are extremely unlikely to represent either recent or frequent colonizations. In terms of dispersal capability and pattern of spatial distribution, they are a mixed lot. *Euphydryas chalcedona* is a good disperser and widespread; *E. editha* is highly colonial but fairly vagile; *S. mormonia* is extremely colonial in the N state, with only three populations known (Mount Eddy, Warners, Ball Mt., all phenotypically different); the various Lycaenids and Hesperiids vary among themselves. *Pieris napi* and *Lycaena nivalis* appear to be very compelling Warner-Ball disjuncts. It is unclear how *L. heteronea* fits into this. The *gravenotata* phenotype does not occur in the Warners, but has a spotty and very local distribution in the N state, strongly suggestive of relictualism; it never seems to co-occur with normal *heteronea*.

The essence of both Croizatian panbiogeography and vicariance biogeography is the premise that congruent distributions in different taxa should be interpreted as reflecting a common historical process. Shapiro (1970) did this with the distributions of sedge-feeding marsh butterflies in the eastern Nearctic, pointing out that a few seemingly similar patterns (*e. g.*, for *Pyrgus communis* Grote) were demonstrably irrelevant. As Humphries and Parenti (1986, p. 87) declare with reference to the biogeography of the Southern Hemisphere, "The finding of a pattern corroborated in whole or in part by numerous other groups of plants and animals invites a general explanation..." The pattern of Warner-Ball Mt. disjunctions leads to a prediction that further floristic and faunistic affinities are to be expected. The high diversity of ecological adaptation and dispersal capability among the taxa so far identified, and the fact that some are very poor candidates for dispersal, reinforce the appearance of real pattern. So does climatology: strong easterly flow, which would carry the Warner biota across Butte Valley to the Ball Mt.-Willow Creek Mt. massif, is very rare, and the topography is overwhelmingly aligned against it.

The most probable explanation of our putative pattern is not recent dispersal and colonization, but a relictual distribution. During the Xerothermic or Hypsithermal interval some 5-6000 yr BP (Axelrod, 1977), warm summers and reduced rainfall caused the elevational life-zone gradients in the northern Sierra to migrate upslope. The subsequent return to somewhat cooler, moister conditions left isolated relict populations of various plants, such as Foxtail Pine (*Pinus balfouriana* Grev. & Balf.) (Mastrogiuseppe, 1972), in northern California and in the high central and southern Sierra Nevada, as the intervening low mountains were unable to sustain populations of them. Similarly, Shapiro (1970) inferred that the distribution of *Plebeius melissa* in the eastern United States was of Xerothermic relict origin. In summary, the butterfly connection between Ball Mountain and the Warners suggests an ancient expansion of the more arid Warner climate, which allowed penetration of eastern Siskiyou County by elements from farther east which largely died out as the Xerothermic yielded to more modern conditions. On Ball Mountain very local microclimates or soil conditions may have permitted the persistence of species or (in *S. zerene*) relict genes in populations. Because this scenario makes specific paleoclimatic predictions, it is potentially testable.

A Comment on Barriers

The relatively low massif of Ball and Willow Creek Mountain separates two different climates and vegetation zones. Table 3 presents some relevant climatological data. Mount Hebron Ranger Station (NOAA #5941, 41°47'N, 122°02'W, 1290 m) has much colder winters (and cooler summer night) than Montague/Siskiyou County Airport in Shasta Val-

Table 3. Climatic comparisons between Mount Hebron Ranger Station (Butte Valley) and Yreka (west side Shasta Valley). Mount Hebron data are frequently unavailable in winter, but data available from local ranchers indicate much colderr winters than at Yreka with occasional minima to -34°C.

	1951-1980 30-year monthly and annual precipitation means (cm)												
	J	F	M	A	M	J	J	A	S	O	N	D	
Mount Hebron Ranger Sta.	3.58	3.02	2.64	2.11	2.46	2.41	0.90	1.32	1.40	2.52	4.24	4.80	31.40
Yreka	9.35	5.51	4.57	2.82	1.96	2.16	1.02	1.60	1.50	3.18	5.94	9.78	47.39
	Monthly temperatures, means (°C)												
Mount Hebron Ranger Sta.[a]	NA	NA	6.15	9.65	6.30	11.65	NA	18.30	12.85	8.50	NA	NA	
Yreka[b]	1.11	4.00	8.83	10.89	13.93	17.00	20.55	19.11	17.55	13.83	9.28	6.39	

Frost-free season, dates between extremes													
	Last spring minimum of					First autumn minimum of					Days between		
	-8.9	-6.7	-4.4	-2.2	0°C	0°C	-2.2	-4.4	-6.7	-8.9	-4.4	-2.2	0°C
Mount HebronRanger Sta.[a]	5.V	29.V	7.VI	29.VI	30.VI	NA	NA	19.IX	20.IX	NA	114	104	NA
Yreka[a]	5.II	12.III	30.V	30.V	30.V	18.IX	9.XI	18.XI	18.XI	18.XII	172	163	111

[a] 1988 data only.
[b] 30-year (1951-80) means.
NA = not available.

ley, or Yreka (NOAA #9866, 41°43', 122°38'. 800 m) across the valley. This is reflected in the presence E of Ball Mt. of elements of the N Great Basin fauna including *C. p. ariane* and *L. rubidus*. (Other elements, *e. g.*, *Pontia beckerii*, *Colias philodice* Godt., *Plebeius melissa*, etc. enter Shasta and Scott Valleys as well.) Similarly, *C. p. boopis*, the *L. xanthoides-editha* intergrades, and *H. lindseyi* and *columbia* behave as W-slope entitites. *Mitoura nelsoni* Bdv. as it occurs on Ball Mt. may be biologically two different entities, but neither Kurt Johnson (pers. comm.) nor I can differentiate them except by ecological context. On the W slope it feeds on *Calocedrus decurrens* Torr.(Cupressaceae) as elsewhere. On the lava flow near the top, and on the lower E slopes and the fringe of Butte Valley, it feeds on juniper. The juniper-feeding populations are on average slightly purpler in habitus than the incense cedar-feeding ones. They may or may not be the same as the very abundant juniper feeders farther E in Modoc Co.; perhaps only biochemical genetics will finally clarify these issues.

The title of this paper calls Ball Mountain a "montane barrier zone." In what sense might it be considered a barrier? There is no evidence that butterflies *cannot* fly across Ball Mountain. It is neither very high nor capped with permanent ice or snow, and during butterfly season it is seldom cloudy before midday. Yet, on a smaller scale, Ball Mountain appears analogous to the Sierran crest as a faunal divide. At Donner Pass (2100 m) both *Coenonympha tullia california* Westwood and *C. t. ampelos* Edwards occur as strays, *ampelos* at least breeds occasionally, but neither persists and no gene flow is likely to occur between them there. Farther N they intergrade (Porter and Geiger, 1988). Similar phenomena occur at Donner in the *Hesperia* "*comma* complex," in *Polites sabuleti*, and in the *Phyciodes campestris* Behr/*montana* Behr complex (Shapiro and Geiger, in preparation). At Ball Mountain we find the *H.*"*comma* complex," *C. tullia*, *C. pegala*, and *Lycaena editha*/*xanthoides* at least behaving in the same ways.

The actual nature of species (or subspecies!) borders - the lines beyond which biological entities no longer persist - is very seldom understood. "Intrinsic barriers to dispersal" (Ehrlich, 1961) tells us little. In butterflies such limitations may be essentially physiological (*Colias philodice*, Shapiro, unpublished data), harking back to C. H. Merriam's "laws" of biogeography (Merriam, 1894). The role of Ball Mt. as a "barrier" is more likely to entail its presence between two contrasting climates, than its physically obstructing access from one to the other. The montane coniferous forest that dominates Ball Mountain, rather than trapping wandering strays, seems to serve as a filter permeable to some species and not to others. It is very remarkable to observe the precise localization of *Polites sabuleti* or *Hesperia* "*comma*" of the *harpalus* phenotype to well-defined areas on the E and S slopes of Ball Mt. when their favored nectar source, *Haplopappus* sp., lines the roads and is in bloom simultaneously all over the mountain. It would be more remarkable to understand it.

The presence of so many species in so small an area seems to represent in this case the conjunction of four factors: proximity of two faunas; attraction of dispersing montane butterflies; the presence of a relict Warner Mountain fauna; and an unusually telescoped vegetation gradient which presents many habitats over short distances. When the richness of the Ball Mountain fauna was first discovered, and the large number of rare species noted, it was initially assumed "mass effect" and collection of strays would account for much of the phenomenon. That possibility seems increasingly remote.

Note added in proof

Since this paper went to press, a collecting trip 6.VII.91 recorded 48 species on Ball Mt., three of them new to the site: *Papilio multicaudatus* (Kirby) (Papilionidae), *Euphilotes enoptes* (Bdv.) ssp. (Lycaenidae), and *Carterocephalus palaemon* (Pallas) (Hesperiidae), all in the Shovel Creek drainage on the E side. This raises the total taxa to 104. This trip also turned up a colony of *Hesperia lindseyi* at Shovel Creek (first record on the E) and established a host plant of *P. anna/ricei* there (*Lotus oblongifolius* (Benth.) Greene, Leguminosae). The complete species list follows: *P. zelicaon, P. eurymedon, P. rutulus, P. multicaudatus, P. clodius, P. beckeri, P. occidentalis, C. eurytheme, C. philodice, A. lanceolata, E. ausonides, C. tulli* nr. *eryngii, C. p. boopis, C. silvestris, D. plexippus, L. lorquini, V. cardui, N. californica, N. antiopa., P. zephyrus, P. campestris, P. mylitta, C. h. segregata, C. palla, E. chalcedona, B. epithore, S. coronis, S. z. conchyliatus, S. c.* nr. *rupestris, S. h. purpurascens, M. nelsoni, I. iroides, L. xanthoides/editha, L. helloides, L. nivalis, P. i. anna/ricei, P. saepiolus, P. icarioides, P. acmon, P. lupini, E. amyntula, G. piasus, C. a. echo, E. enoptes, P. communis, E. persius, C. palaemon, H. lindseyi.*

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